GROWTH OF OYSTERS WITH DAMAGED SHELL-EDGES

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During the past few years several papers have appeared dealing with the structure and other characteristics of oyster shells. Medcof (1944) discussed the structure, deposition and quality of the shell of the American oyster, *Crassostrea virginica*, while Korringa (1951a, 1951b) described at length the structure of the shell of the European oyster, *Ostrea edulis,* and also considered it as a habitat harboring numerous species of the epifauna of oysters. Korringa also incorporated in his papers an extensive review of the literature on shells of other oysters and related mollusks. Owen (1953) commented on the shells of lamellibranchs but confined himself almost exclusively to the matter of shell form.

No systematic observations, however, had been made to determine whether damage to oyster shells, such as breaking off their edges, would result in a more rapid growth, which would partly or wholly compensate for the loss caused by the breakage. The present studies were undertaken because we thought that information on this subject would be of both biological and practical significance.

A review of the literature shows that only the articles of Glaser (1903, 1905a, 1905b) and Nelson (1921) discussed a subject related to our problem. Glaser found that mis-shaped oysters, *Ostrea virginica* (now *Crassostrea virginica*), which had grown under unfavorable, overcrowded conditions, would eventually attain normal shape if replanted with ample room for unobstructed shell-growth. He also found that oysters, the growth of which had been inhibited by physical obstruction, would show rapid growth of shell in the affected areas after the obstruction was removed. Nelson (1921) later came to the same conclusions.

Breaking of shell-edges is common when heavy dredges are used for gathering oysters, as is the practice in Long Island Sound and in many other areas where the oyster beds are located at a considerable depth. The damage is especially severe if the oysters are dredged during periods when the new shell-growth is still thin and brittle. In Long Island Sound the most rapid increase in the length of oysters takes place during May, June and July, representing, respectively, 22.57, 19.03 and 22.12 per cent of the total annual increment (Loosanoff and Nomejko, 1949). The oysters dredged during that period usually have a considerable part of the new shell-growth broken off. Since in some areas the oysters may be handled several times annually, and because each time many of them may have the edges broken off, the accumulated loss of shell may be quite significant.

Our first experiment was begun July 18, 1946. Fifty oysters were divided at random into two equal groups. The oysters of the first group, designated as the control, were measured to determine their length, representing the greatest anterior-posterior dimension (Table I). The oysters of the second group were measured in a similar way, but after the initial measurements had been made the edges of their shells were filed off.

TABLE I

Original mean length and increase in mean length of shells of normal oysters and of oysters the shell-edges of which were filed off. Milford Harbor, 1946, 1947 and 1949. Measurements in millimeters

Group	Original length	Length after filing	Decrement due to filing	Length at end of season	Increase over		Per cent increase over	
					Original length	Filed length	Original length	Filed length
1946								
Control	69.5	—	—	91.7	22.2	—	31.9	—
Damaged	68.7	61.7	7.0	89.6	20.9	27.9	30.4	45.2
1947								
Control	92.7	—	—	102.9	10.2	—	11.0	—
Damaged	91.4	84.5	6.9	104.4	13.0	19.9	14.2	23.6
1949								
Control	85.4	—	—	112.8	27.4	—	32.1	—
Damaged	83.4	79.7	3.7	111.1	27.7	31.4	33.2	39.4

In filing, the shell material was removed all the way around the "bill" instead of only in one place, near its end (Fig. 1). The filing reduced the mean length of the shells by about 7.0 millimeters (Table I). The filed-off material consisted not only of recently-formed, thin and transparent shell but also of the thicker, old portion, some of which may have been formed the preceding year. After the filing the oysters were re-measured, and both groups were placed in wire trays, which were suspended side by side in Milford Harbor.

Since the filing was done by hand and slowly, the oysters had enough time to contract the edges of the mantle, avoiding injury to it. Because of this the amount of mantle tissue remained the same as before the filing, thus still possessing the original area of secretory surface for the formation of new shell.

For clarity of description, all the oysters, or groups of oysters, the shells of which were filed off in these experiments, will be called the damaged oysters, while the unfiled ones will be referred to as the control. The oysters used in these experiments were adults, three to six years old.

On December 6, 1946, when the water in Milford Harbor was already cold enough to stop shell-growth, the oysters were again examined. The measurements showed that during the period of the experiment the damaged oysters had added more new shell-growth than the controls. In general, since the date of filing, the mean length of the damaged oysters showed an increase of 27.9 mm., while that of the controls was only 22.2 mm.

The experiment was repeated again in the summer of 1947 using 50 individually-marked oysters for each group (Table I). The shells of one group were filed off on August 14, and then both the damaged and the control oysters were suspended together in the same tray in Milford Harbor. After the beginning of the hibernation period the oysters were again examined. It was found that, as indicated by the increase in length, the damaged oysters had not only added more

new shell-growth than the controls, but had actually outgrown them by the end of the season.

In 1947 both groups of oysters grew less than those used in 1946. This can be attributed to several considerations: first, the 1947 experiment was begun approximately one month later than that of 1946. Secondly, the oysters used in 1947 were considerably larger than those used in 1946 and their rate of growth could be expected to be slower than that of the smaller and younger oysters (Loosanoff, 1947). Finally, since the locations of the trays in which the oysters were suspended varied in the different years, the oysters may have been subjected to a somewhat different set of ecological conditions.

The experiments conducted in 1946 and 1947 showed conclusively that the oysters, the shell-edges of which had been filed off, compensated for this loss by forming new shell at a more rapid rate than the uninjured oysters living under identical conditions. However, since the experiments of these two years were not initiated at the beginning but approximately in the middle of the growing period, the experiments were repeated once more, starting in the spring when the oysters come out of hibernation, and continuing until late fall when the water again becomes too cold for oysters to grow.

On April 14, 1949, two groups, each composed of 110 individually-marked oysters, were treated as described above, and suspended in trays. Because the experiment commenced at the beginning of the shell-growing period, which in our waters usually occurs during the second half of April, the parts of the shells that were filed off consisted exclusively of old shell material that had been formed the year before. The restoration of that portion of the shell could be considered, therefore, as a true regenerative activity on the part of the oysters.

Final examination and measurements of the oysters were made on October 27. Three oysters were found dead in the control group but none in the damaged one.

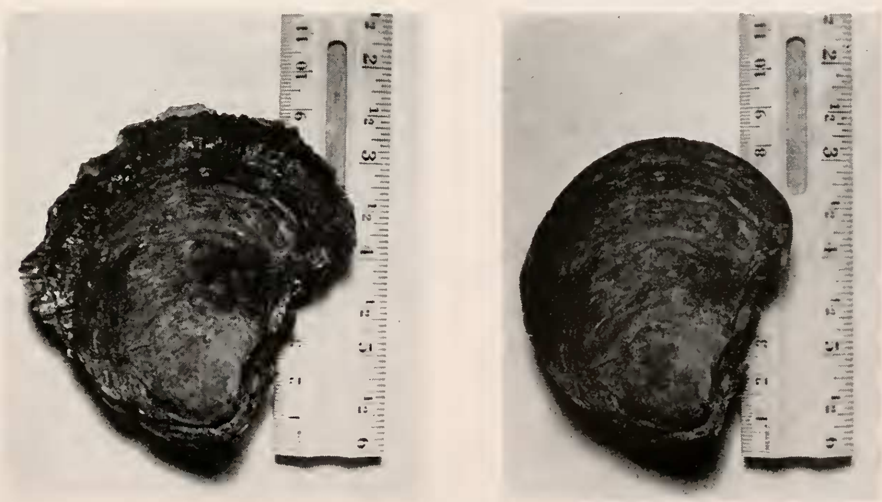

FIGURE 1. Photographs of the same oyster taken before and after the shell-edges were filed off.

The measurements showed that the damaged oysters again increased in length more than those of the control group (Table I).

Since the shell-edges of oysters may be broken off any time during the year, an experiment was devised to determine whether the tendency to compensate for such damages is present throughout the growing season, which extends from April to November (Loosanoff and Nomejko, 1949). The experiment was conducted as follows: On April 8, 1948 oysters that came from the same source were divided at random into five groups each containing 55 individuals, and the mean length of the oysters of each group was determined (Table II). The shells of Group 1, designated as the control, were not filed off during the entire period of observation. The shells of Group 2, however, were filed off on April 8, to provide information on the growth of oysters, the shells of which would be broken early in the spring, at the very beginning of the growing period. After filing, the oysters of Group 2 were again measured. All five groups were then suspended in wire trays in Milford Harbor, presumably under identical conditions.

As the season progressed, the oysters of Groups 3, 4 and 5 had their shells filed off. Each time measurements were taken before and after filing (Table II). Group 3 was filed off on July 13, Group 4 on August 9 and Group 5 on September 7. Thus, the entire season was roughly divided into four periods. Each time a group had its shells filed off and the length recorded, the length of the control group was also measured.

During this experiment 46 oysters were either lost overboard, died, or had their shells broken accidentally, thus becoming ineligible for further observations. The loss was especially serious in our control group when approximately half of it was lost near the end of the experiment. Nevertheless, 229 oysters were still available and our statistical analysis was based on these individuals. The number of oysters remaining in each group was as follows: Group 1—26; Group 2—54; Group 3—54; Group 4—51; and Group 5—44.

TABLE II

Original mean length of five groups of oysters and increase in mean length of normal oysters and of the oysters the shell-edges of which were filed off during different months of the growing period. Milford Harbor, 1948. Measurements in millimeters

Date	Groups				
	1	2	3	4	5
April 8, 1948	88.01	84.26* 81.70**	84.41	82.14	82.42
July 13, 1948	96.95	—	95.56* 90.68**	—	—
August 9, 1948	101.61	—	—	96.01* 91.79**	—
September 7, 1948	106.87	—	—	—	104.19* 99.26**
November 29, 1948	114.61	110.83	113.09	109.16	110.68

* Measurements before filing.
** Measurements after filing.

TABLE III

Decrements and increments of mean length of shells of normal oysters and of the oysters the shell-edges of which were filed off during different months of the growing period. Milford Harbor, 1948. Measurements in millimeters

Aspects studied	Groups				
	1	2	3	4	5
Decrement due to filing	—	2.56	4.88	4.22	4.93
Actual Length Increment (final length less initial length)	26.60	26.57	28.68	27.02	28.26
Per Cent Actual Length Increment	30.22	31.53	33.98	32.90	34.29
Total Length Increment (Actual Length Increment plus decrement due to filing of edges)	26.60	29.13	33.56	31.24	33.19
Per Cent Total Length Increment	30.22	34.57	39.76	38.03	40.27
Increase in length since filing, in millimeters	—	29.13	22.41	17.37	11.42
Corresponding increase of control, in millimeters	—	26.60	17.66	13.00	7.74
Per cent increase in length since filing	—	35.65	24.71	18.92	11.51
Corresponding per cent increase of control	—	30.22	18.22	12.79	7.24

Regardless of the supposedly random sorting of the oysters at the beginning of the experiment into five groups we found later that the control, Group I, had a somewhat higher mean length than the other four groups (Table II). Analysis of variance showed that the differences in the initial length were significant beyond the .05 level. Therefore, to avoid in the analysis difficulties that would result from a disparity in the initial length, we decided to base the analysis of the amount of growth, shown by the different groups throughout the entire period of the experiment, not on the final length but on the difference between the initial and final lengths. This difference was termed the Actual Length Increment (Table III).

The analysis of variance, to test for homogeneity of the five groups on the basis of their Actual Length Increments, showed no significant difference among the groups. The conclusion was formed, therefore, that by the end of the growing period the damaged oysters showed approximately the same length increment as would have been expected of them if their shells had not been filed off. It should be remembered, however, that the Actual Length Increment does not include the increment needed to make up for the loss in length due to filing of the shells. If these two increments were combined to form the Total Length Increment (Table III), this would clearly show that all the damaged groups of oysters added more new shell and consequently must have increased in length faster during certain intervals than the control.

The stimulation caused by filing of the shells did not induce a significant increase in length beyond that of the oysters in the control group. The observations showed that, regardless of when during the growing period the edges of the shells

were filed off, the oysters grew just enough to compensate for this loss and then added to it the normally expected length increment.

Another measure considered in connection with our data was the Total Length Increment which, as already mentioned, consisted of the Actual Length Increment plus the decrement due to filing of the shells (Table III). (For the control group, obviously, the Actual Length Increment and the Total Length Increment were identical.) The analysis of variance for the four damaged groups on the Total Length Increment indicated that there were significant differences among the groups. This was especially true for Group 2 which showed a smaller Total Length Increment than the other damaged groups. However, this was to be expected because the decrement due to filing varied from group to group. Thus, the oysters of Group 2, which were filed earliest in the growth period, had the smallest decrement and, therefore, had to grow less in total length to achieve the same final length as the oysters of the other groups (Tables II and III).

It was thought that there might be a definite relationship between the amount of shell removed and the final length reached. However, it was established that the amount of damage, within our experimental scope, was not an important factor, that is, regardless of how great or slight the damage was, the individual oysters appeared to be stimulated only to the extent of compensating for the loss in length and then adding whatever additional increment would be expected under normal conditions. In other words, by breaking off more shell along the edges, the oysters could not be induced to reach proportionately greater length by the end of the growing season.

Although the experiments showed that breaking of shell-edges induces oysters to grow faster in length, we had no information concerning the rate at which such an increase proceeded. Because we had made no measurements on the oysters of Groups 2–4 after their shells had been filed, except the final one at the end of the growing period, there were no data for ascertaining the shape of the growth curve after the damage to the shells. It was thought, nevertheless, that since the damaged oysters showed practically the same Actual Length Increment as the control, the stimulating effect of shell-damage did not induce the oysters to grow at an accelerated rate throughout the remainder of the growing period. This was well illustrated by the oysters of Group 2, the shells of which were injured at the beginning of the growth period. This group, subsequently, had approximately eight months in which to grow at the accelerated rate if such rate were a reality. Nevertheless, the Actual Length Increment of these oysters not only did not exceed those of the three other damaged groups, but their Total Length Increment was the smallest (Table III).

Theoretically, there were at least two hypotheses regarding the rate of growth of oysters after damage to their shells. First, it could be assumed that following shell-damage the growth would continue at a somewhat accelerated but, nevertheless, even rate throughout the entire remaining portion of the growing period. The second possibility was that immediately after the damage the growth would proceed at a rapid rate but then, after sufficient growth had been added to the shell-edges to compensate for the original loss, the growth would decrease to the normal rate corresponding to that of the undamaged oysters. We thought the latter hypothesis was more probable because Group 5, which was damaged late

in the growing period, still came up to parity with the other groups in the length increment, thus indicating very rapid growth within a short period. However, to solve this matter definitely we carried on the following experiment:

Two groups of oysters were selected from a common source on May 21, 1954. The average length and width of the oysters of both groups were identical, being 80.6 and 64.5 mm., respectively. After that the shells of one group were filed off, reducing the average length to 77.0 mm. and average width to 60.0 mm. Both groups were then kept under the same conditions. A week later the average length and width of the control oysters were 81.0 and 65.0 mm., respectively, while similar dimensions of the damaged oysters were 79.5 and 62.5 mm. After two weeks the length and width of both groups became identical, being 82.0 and 66.5 mm., respectively, thus indicating that during this short period the oysters with filed shells had caught up with the control oysters. From then on the oysters of the two groups grew at approximately the same rate, showing no significant differences. This experiment has proven, therefore, that the second hypothesis was correct, namely, that in injured oysters the growth proceeds at a rapid rate for a brief period immediately after damage and then decreases.

The rapid growth of the new shell, representing "repair" or regeneration of the portion of the old one removed by filing, is probably due chiefly to the fact that the mantle of the oyster can now protrude farther along the edges of the shell. Because of this the secretory activities of the mantle involved in the formation of the edges of the shell are accelerated. The accelerated growth continues until the shell has grown enough to establish the normal ratio between the size of the oyster body and the length and width of the shell. After that the increase in length continues at approximately the same rate as in the undamaged oysters.

A rapid "repair" of the edges of shells is possible only if the oyster itself, especially its mantle, remains uninjured. If the mantle is injured, the oysters may not be able to show any increase in length until they recover. We have observed a number of such cases under laboratory conditions and also in nature. The best example of the latter was the condition of the Long Island Sound oysters following the extremely severe and prolonged storm of November, 1950. During this storm the oysters were rolled on the bottom by the wave action for many hours and with such force that the shell surfaces acquired almost a polished appearance, while the edges of the shells were rubbed off to such an extent that often the soft parts of the oysters protruded between them. Many oysters died because of injuries, which usually involved the mantle tissue. Those that survived did not resume normal growth but developed into stunted oysters with thick, irregular shells. Oysters of this type are still found in Long Island Sound four years after the storm.

The observations discussed in this paper are concerned almost exclusively with growth of shells as indicated by length measurements. They do not cover other aspects of growth and we know that it is possible that while in some of our experiments the new, thin shell-growth indicated an increase in length, the weight and volume of the oysters may have been smaller than before the shells were filed. Nevertheless, our auxiliary experiments, designed to ascertain the rate of growth immediately after filing, showed that after the edges of the shells had been filed, as shown in Figure 1, the growth in width proceeded at the same rate as the growth in length. This suggests that breakage of shell-edges is repaired by growth of

the same pattern regardless whether it is length or width that is involved in the damage.

Our studies represent only initial steps toward understanding various aspects of the growth of damaged oyster shells. The next experiment, which suggests itself, should consist of studying the growth of oysters, the shell-edges of which were broken several times during the growing period. The growth curve of repeatedly damaged oysters should differ considerably from that of normal oysters, or of oysters the shell-edges of which were broken only once during the season.

Another aspect of these studies could be directed toward ascertaining whether the growth of oysters of different ages and sizes, damaged in the same manner, would differ significantly from that of the oysters on which the present conclusions are based. Because we already know that during the first years the increases in length, width and depth of an oyster proceed at different rates than later in life (Loosanoff, 1947), we may assume such a difference to exist. This assumption would be in agreement with the observations of Glaser (1905b) who found that the recuperative power of overcrowded, mis-shaped oysters varies with age, young individuals recovering their normal shape more rapidly than old ones.

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Summary

1. These experiments, based on length measurements, showed that oysters, the shell-edges of which were broken off, compensate for this loss by forming new shell at a more rapid rate than undamaged oysters living under identical conditions.

2. Damage to shells does not stimulate oysters to grow at an accelerated rate throughout the remainder of the growing period. Immediately after the damage they grow rapidly to compensate for the loss and then continue to grow at the usual rate to add to their length the normally expected annual increment. Thus, no relationship was found between the amount of shell removed and the final length reached.

3. The ability of oysters to repair broken shell-edges and still grow to about the same length as undamaged oysters remains the same regardless of when during the growing season (April 8–September 7) the shells are broken.

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